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Systematic relationships of the Verdin: Skeletal evidence (Aves: Passeriformes)

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Abstract.—Recent systematic treatments have placed the Verdin (*Auriparus flaviceps*) in 4 different families. The skeleton of the Verdin is compared with 17 species of 10 genera variously supposed to be close relatives. In 19–20 of 22 skeletal characters, *Auriparus* is close to *Anthoscopus* and *Remiz*, as contrasted with 5–9 in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Psaltriparus*, and *Coereba*. This tends to confirm external anatomy, behavior, and nest characters; the species belongs with the penduline tits, Remizidae.

The relationships and systematic position of the Verdin (*Auriparus flaviceps*) have been variously hypothesized. Until recent years it was placed with the tits in the family Paridae (for example, A.O.U. Check-list, 1957). Snow (1967) segregated it in Remizidae, the penduline tits, along with the Old World genera *Remiz*, *Anthoscopus*, and *Cephalopyrus*. A similar arrangement was followed by Cramp & Perrins (1992). Taylor (1970) thought it belonged in Emberizidae, near *Coereba*. Harrap & Quinn (1995) allowed only a subfamily (of Paridae) for the penduline tits and Verdin. The most recent A.O.U. Check-list (1998) placed it in Remizidae, as did Phillips (1986) and Sheldon & Gill (1996). Sibley & Monroe (1990) placed it in the family Certhiidae, subfamily Polioptilinae, along with the gnatcatchers and gnatwrens, *Microbates*, *Rhamphocaenus*, and *Polioptila*. Among these references, only Cramp & Perrins and Harrap & Quinn gave characterizations based on behavior, nest, and external anatomy. Sibley & Monroe's action was based on DNA study by Sibley & Ahlquist (1990). As Phillips remarked, "this gives the reader plenty of choice!"

Previous studies of the Verdin skeleton were those of Lucas (1890), Beecher (1953), and George (1962). Lucas found little difference between *Parus* and *Auriparus*, but noted a more incomplete interorbital septum and a smaller mandibular foramen in the latter, concluding that they were close relatives. Beecher (1953) mentioned only one differential skeletal character between his Remizinae (*Anthoscopus* and *Auriparus*) and the other Paridae—the ectethmoid foramen was single rather than pinched. George (1962), studying only the hyoid, put in one group all of the genera I compared, except *Coereba*.

Recent classifications of this group of birds are based on nuclear DNA or on external anatomy, nest, and behavior. Addition of a skeleton character set should improve the situation. I have studied skeletons of all families and nearly all subfamilies of Oscines (Webster & Goff 1979; Webster 1992, 1994, 1997; Webster & Webster 1999). In the present paper the skeleton of *Auriparus* is compared in detail with most of its supposed close relatives—of Polioptilidae *Microbates*, *Rhamphocaenus*, and *Polioptila*; of Aegithalidae (long-tailed tits) *Aegithalos* and *Psaltriparus*, of Remizidae *Remiz* and *Anthoscopus*; of Paridae (true tits) *Parus* and *Melanochlora*; of Emberizidae *Coereba* (Bananaquit).

Table 1.—Results of detrended correspondence analysis ordination. Values are the scores of the skeletal parameters on each of the DCA axes. The last rows indicate the eigenvalues of the axes and cumulative coefficients of determination of the correlations comparing ordination distances between bird species and Euclidean distances in the original data.

Variable	Axis 1	Axis 2	Axis 3
Skull length	21	−185	−21
Premaxilla length/width	−34	123	134
Tibiotarsus length/ulna length	−70	92	−130
Tibiotarsus length/humerus length	−68	80	−68
Tibiotarsus length/femur length	53	157	−44
Ulna length/femur length	203	42	159
Humerus length/femur length	213	16	101
Length/width of interpalatine process	−53	34	76
Length/width of transpalatine process	107	194	8
Length/width of zygomatic process	−12	72	216
Length/width of retroarticular process of mandible	147	250	−100
Length/width of pseudotemporal process of mandible	95	−37	−92
Pneumotricipital fossa of humerus: percent depth of the dorsal fossa to the depth of the ventral fossa	179	−61	−47
Tibiotarsus length/tarsometatarsus length	208	84	−35
Length/width of tarsometatarsus	−61	−24	62
Tarsometatarsus length/skull length	−62	−6	5
Basal width/narrowest width of internal process of mandible	157	28	86
Height/width of basihyale	100	−27	134
Eigenvalue	0.138	0.021	0.009
Coefficient of determination	0.766	0.771	0.832

Methods

Most elements of the skeleton were perused; 39 characters were tabulated. Twenty-two characters are analyzed below; 18 of these are numerical enough to be analyzed statistically. Of the 17 characters not analyzed, 12 were too erratic within species, 4 were too uniform within the entire group, and one had too many missing data because of broken or missing bones. Within the statistically analyzed data, in one case, because of missing bones, a datum from a congeneric species was substituted. This was height/width of the basihyale, where the datum for *Aegithalos concinnus* was used for *A. caudatus*. The four characters not analyzed statistically are marked with an asterisk (*) in the results. In each species where more than one specimen was studied, the number given is the mean of measurements or of ratios of measurements of all specimens. Unfortunately, skeletons of three possibly related genera (*Psaltria*, *Cephalopyrus*, and *Sylviparus*) were not examined, nor were several other species of examined genera (mostly *Parus*).

Eighteen quantitative characters (Table 1) were used in a detrended correspondence analysis (DCA) ordination (Gauch 1982). All data were converted to ranks, but analyses run on non-transformed data produced qualitatively similar results. Analyses were performed using PC-ORD (McCune & Mefford 1997).

Skeletal Specimens Examined

Microbates collaris 3: Peru 2 (LAS121393, LAS111606), French Guiana 1 (RON 125903).

Microbates cinereiventris 3: Costa Rica 1 (LAS63107), Colombia 1 (USNM 428228), Peru 1 (LAS111604)

Rhamphocaenus melanurus 3: El Salvador 1 (MVZ86284), Colombia 1 (MVZ 141823), 1 not recorded

Polioptila caerules 6: California 2 (MVZ

150800, MVZ69803), Florida 2 (KUN 61089-90), 2 not recorded.

Polioptila plumbea 2: Panama 1 (USNM 430601), Colombia 1 (DEL60776).

Aegithalos caudatus 4: Denmark 1 (LAS 122975), Poland 1 (UFL28538), Russia 2 (UFL28539, UMI33470).

Aegithalos concinnus 3: Captive 2 (BM·51996·53·1, BM·S1999·21·1), China 1 (USNM318461).

Psaltriparus minimus 8: California 2 (DEL49825, KUN23384), Arizona 1 (KUN19035), Oklahoma 1 (CARN9285), Texas 3 (RON125997-8, RON126994), 1 not recorded.

Remiz pendulinus 2: France 1 (UFL28551), Israel 1 (USNM502125).

Anthoscopus caroli 3: Kenya 1 (LAS 28083), Zimbabwe 2 (RON114598, (CARN15912).

Anthoscopus parvulus 1: Ghana (UMI 221025).

Anthoscopus minutus 4: Namibia 1 (RON156922), Republic of South Africa 3 (DEL63150-1, DEL63213).

Auriparus flaviceps 12: California 4 (KUN 37094, KUN37101), (UMI151760-1), Arizona 6 (UMI159183, YALE10266, YALE10268, YALE10279, YALE10281-2), Texas 2 (USNM554365, RON 129858).

Parus atricapillus 7: Kansas 2 (MVZ 52869, MVZ60955), Connecticut 5 (YALE5843-4, YALE10619, YALE 5657, YALE5825).

Parus major 2: India 2 (RON125618-9).

Parus bicolor 4: New Hampshire 1 (MCZ 7735), Massachusetts 1 (MCZ7333), Florida 2 (UFL22081, UFL28630).

Melanochlora sultanea 1: Malaya (BM·S1969·1·169).

Coereba flaveola 9: Mexico 2 (RON 112083, RON112141), Costa Rica 2 (both CAS number not recorded), Colombia 2 (DEL61050, DEL63019), Bahamas 1 (BM number not recorded), Grand Cayman 1 (BM1904·8·5·2), 1 not recorded.

Certhia familiaris 2: England 1 (USNM 49824), France 1 (USNM number not recorded).

Certhia americana 11: Ontario 1 (RON 127589), United States 5 (FM290725, FM291213, YALE6730, YALE10682-3), 5 not recorded.

Certhia brachydactyla 1: Greece (USNM 488800).

Certhia himalayana 1: China (USNM 319349).

Certhia discolor 1: Thailand (USNM 343078).

Salpornis spilonotus 2: India 2 (RON 125277, RON125624).

Campylorhynchus brunneicapillus 1: California (KUN19009).

Thryothorus ludovicianus 2: Indiana 2 (both CAS, number not recorded).

Troglodytes troglodytes 2: England 1 (BM1984·47·2), Indiana 1 (INST number not recorded).

Table 2.—Zygomatic process of the squamosal. Length/width ratio.

Polioptila	1.3–2.7
Rhamphocaenus	2.2
Coereba	1.9
Microbates	1.2–1.8
Remiz	1.4
Anthoscopus	0.5–1.2
Parus	0.4–1.2
Psaltriparus	1.1
Aegithalos	0.8–1.1
Auriparus	1.0
Melanochlora	0.6

Results

The retroarticular process of the mandible was long (4–5.5 times as long as wide) in *Remiz*, *Anthoscopus*, and *Auriparus*; moderate (2.4) in *Psaltriparus*; short (0.7–1.3) in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Parus*, and *Melanochlora*: moderate to short (1.0–2.6) in various subspecies of *Coereba*.

The zygomatic process of the squamosal was short in *Auriparus*, in contrast with the gnatcatchers, gnatwrens, and Bananaquit (Table 2).

Table 3.—Tricipital fossa of humerus in some passeriform genera. Numbers in the columns are numbers of specimens examined with this characteristic. Percentages are the proportions of the depth of the dorsal fossa to the depth of the ventral fossa. In the fifth column the septum between the two fossae is prominent except where marked [r], where it is a low ridge.

	30%	40–50%	70–90%	100%; septum complete	100%; septum incomplete (= combined fossae)
Microbates	5	1			
Rhamphocaenus	3				
Polioptila		6	2		
Aegithalos		3	3		
Psaltriparus			6	1	1
Remiz			2		
Anthoscopus			6		2
Auriparus			9	2	1
Parus			2	11[r in 1]	
Melanochlora			1		
Coereba			3	2[r]	4

A completely or partially bony nasal septum was present in all of *Remiz*, *Anthoscopus*, and *Coereba*, seven of 12 specimens of *Auriparus*, and seven of 13 *Parus*. In contrast, there was no bone in the septum in *Rhamphocaenus*, *Polioptila*, *Aegithalos*, *Psaltriparus*, and *Melanochlora* and very little (one specimen) or none (five specimens) in *Microbates*.*

The ectethmoid foramina were double in *Parus* (pinched in two specimens), *Melanochlora*, and *Coereba*; single in *Aegithalos*, *Remiz*, *Anthoscopus*, and *Auriparus*; an intermediate condition, pinched, or variously pinched or single in *Microbates*, *Rhamphocaenus*, *Polioptila* and *Psaltriparus*.*

The transpalatine process at the caudolateral angle of the palatine was short (0.3–1.4 times as long as wide) in *Polioptila caerulea*, *Microbates cinereiventris*, *Aegithalos*, *Parus*, and *Melanochlora*; moderate (2.1–2.6) in *Rhamphocaenus*, *Polioptila plumbea*, and *Psaltriparus*; long (3.0–10.4) in *Remiz*, *Anthoscopus*, *Auriparus*, *Microbates collaris*, and *Coereba*. (In *Coereba*, seven specimens averaged 10.4, but in two the entire caudolateral part of the palatine was absent.)

The interpalatine process was moderate in size and shape (1.1 to 3.2 times as long as wide) in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, and *Coereba*; but very small and slender (3.0) or short (1.0) in *Remiz*; absent or a slight bump in three specimens or moderate in four of *Psaltriparus*; and absent or a slight bump in *Anthoscopus*, *Auriparus*, *Parus*, and *Melanochlora*.

The pneumotricipital fossa of the humerus in all specimens was double or combined (Table 3). In *Microbates*, *Rhamphocaenus*, and most *Polioptila* the dorsal fossa was only 30–50% as deep as the ventral fossa. In *Aegithalos* the dorsal fossa was 50–70% as deep as the ventral fossa and separated by only a step-down. In *Remiz* and *Melanochlora*, and in most *Psaltriparus*, *Anthoscopus*, and *Auriparus* the dorsal fossa was 70–90% as deep as the ventral fossa and separated by only a step-down. In nearly all *Parus* the fossae were equally deep and separated by a prominent medial bar. In *Coereba* the fossae were equally deep and combined in most specimens. (Bock 1962, Webster 1997.)

The interorbital septum was much more extensively bony in *Parus* and *Melanochlora* than in the other ten genera. Lucas (1890) mentioned this character.*

The premaxilla length/width ratio was high (2.6–4.2) in *Microbates*, *Rhamphocaenus*, and *Polioptila*; moderate to high

Table 4.—Tibiotarsus/tarsometatarsus, ratio of length.

Microbates	1.2
Rhamphocaenus	1.2
Polioptila	1.2
Aegithalos	1.3–1.4
Psaltriparus	1.3
Anthoscopus	1.4–1.5
Auriparus	1.4
Parus	1.4
Coereba	1.4
Remiz	1.5
Melanochlora	1.5

Table 5.—Length of skull in mm.

Melanochlora	23.8
Rhamphocaenus	18.6
Microbates	18.5–19.4
Parus	17.6–20.2
Coereba	17.4
Auriparus	15.4
Remiz	15.3
Polioptila	15.0–15.6
Psaltriparus	14.5
Aegithalos	14.3–15.5
Anthoscopus	12.9–14.0

(2.0–3.2 in various subspecies) in *Coereba*; low (1.4–1.8) in the other seven genera (*Auriparus* 1.5).

Shape of the basihyale in these 11 genera varied clearly in two ways. In *Coereba* height at the midpoint was 3.4 times width, whereas in other genera it varied only from 0.7 to 1.2 (George 1962). In all nine specimens of *Coereba*, two of nine *Auriparus*, and five of ten *Parus* the rostral end of the basilhyale was sagitate, whereas in the rest the rostral end was blunt with projecting corners absent or nearly so.*

The ratio of length of tibiotarsus/humerus was high (1.9–2.0) in *Microbates*, *Rhamphocaenus*, *Aegithalos*, and *Psaltriparus*. In *Polioptila* it was low or moderate (1.7–1.8). In the other six genera it was low (1.5–1.7).

The ratio of length of tibiotarsus/tarsometatarsus was higher in *Auriparus* than in the gnatwrens, gnatcatchers, and long-tailed tits (Table 4).

The ratio of tarsometatarsus length/skull length was high (1.1–1.2) in *Microbates*, *Rhamphocaenus*, *Polioptila*, *Aegithalos*, and *Psaltriparus*; low (1.0) in the other six genera.

The ratio of length/width of the tarsometatorsus was high (13.6–14.5) in *Microbates*, *Rhamphocaenus*, and *Polioptila*; fairly high (12.0–13.7) in *Aegithalos* and *Psaltriparus*; moderate (10.8) in *Coereba*; low (7.7–9.5) in *Remiz*, *Anthoscopus*, *Auriparus*, *Parus*, and *Melanochlora*.

Length of the skull was used as a measure of size. *Auriparus* was smaller than the gnatwrens, tits, and Bananaquit (Table 5).

Ratio of tibiotarsus length/ulna length. Range in the 18 species was from 1.20 in *Melanochlora* to 1.72 in *Microbates collaris* with *Microbates*, *Rhamphocaenus*, *Aegithalos*, and *Psaltriparus* higher than the rest.

Ratio of tibiotarsus length/femur length. Range was from 1.68 in *Melanochlora* to 2.03 in *Aegithalos caudatus* and *Psaltriparus* with *Aegithalos* and *Psaltriparus* distinctly higher than the rest.

Ratio of ulna length/femur length. Range was from 1.06 in both species of *Microbates* to 1.42 in *Anthoscopus parvulus*. *Rhamphocaenus*, like *Microbates*, was distinctly low; *Aegithalos*, *Psaltriparus*, and *Polioptila plumbea* were the next lowest.

Ratio of humerus length/femur length. Range was from 0.93 in *Microbates collaris* to 1.21 in *Anthoscopus parvulus*. *Rhamphocaenus* and *Microbates* were lower than the rest.

Internal process of mandible, ratio of width at base/width at narrowest point. Range was from 2.7 in *Microbates collaris* and *Coereba* to 4.5 in *Remiz*. *Microbates cinereiventris* and *Aegithalos caudatus* were next to the lowest.

Pseudotemporal process of mandible, ratio of length/width at base. Range was from 0 (process absent) in *Polioptila plumbea* and *Anthoscopus parvulus* to 0.8 in both species of *Aegithalos*. A prominent process

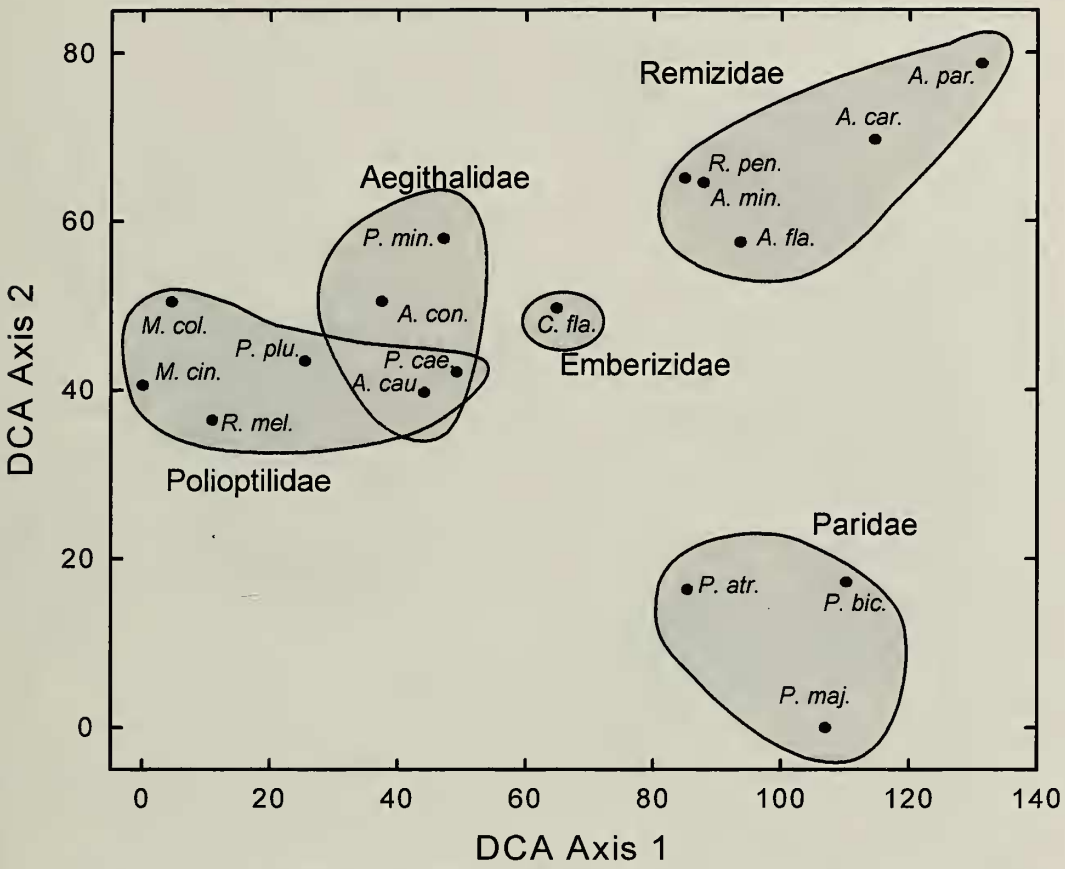

Fig. 1. Results of the detrended correspondence analysis (DCA) of 18 species of songbirds showing the first two DCA axes. Symbols are: M.cin—*Microbates cinereiventris*; M.col—*M. collaris*; R.mel—*Rhamphocaenus melanurus*; P.cae—*Polioptila coerulea*; P.plu—*P. plumbea*; A.cau—*Aegithalos caudatus*; A.con—*A. concinnus*; P.min—*Psaltriparus minimus*; R.pen—*Remiz pendulinus*; A.car—*Anthoscopus caroli*; A.par—*A. parvulus*; A.min—*A. minutus*; A.fla—*Auriparus flaviceps*; P.atr—*Parus atricapillus*; P.maj—*P. major*; P. bic—*P. bicolor*; M. sul—*Melanochlora sultanea*; C.fla—*Coereba flaveola.*

(0.7) was also found in *Parus major* and *Coereba.*

Sibley & Ahlquist (1990) and Sibley & Monroe (1990) proposed a fairly close relationship between the Verdin (together with the gnatwrens and gnatcatchers) and the creepers (*Certhia* and *Salpornis*) as well as the wrens (Troglodytidae). I compared skeletons of the creepers and wrens with the 11 genera treated in detail above on all but seven of those 39 characters. Several characters showed differences; these two seem trenchant: height of the basihyale at its midpoint was 2.0 to 2.5 times width in *Troglodytes* and *Certhia*; 1.0 in *Campylorhynchus*, *Thryothorus*, and *Salpornis*. The pneumotricipital fossa of the humerus lacked a dorsal fossa in *Campylorhynchus*; the dorsal fossa was 30% or less the depth of the ventral fossa in *Thryothorus*, *Troglodytes*, *Certhia*, and *Salpornis* (Table 3). These observed character states (as also those given above for 11 genera) agree with the tabulations of George (1962) for the basihyale and Bock (1962) for the pneumotricipital fossa except for the basihyale of one wren (*Troglodytes*).

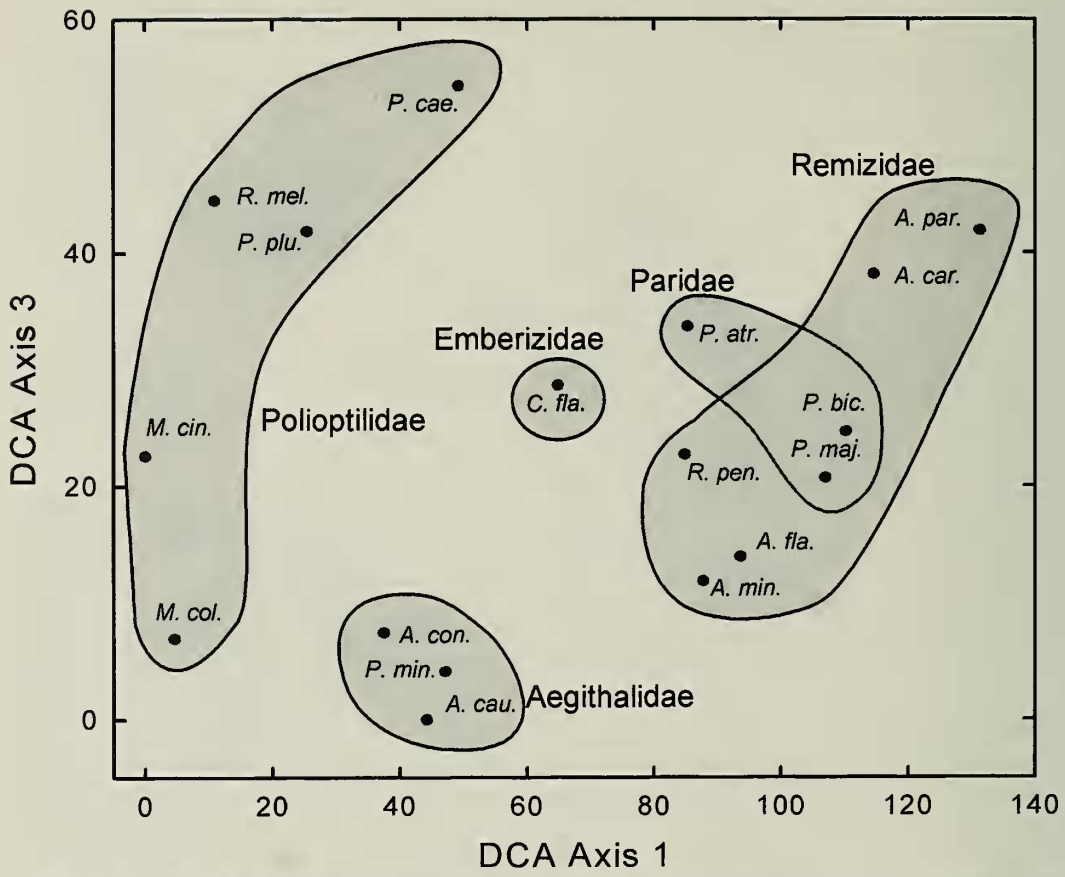

Fig. 2. Results of the detrended correspondence analysis (DCA) of 18 species of songbirds showing the first and third DCA axes. Symbols as in Fig. 1.

Discussion

Results of the DCA ordination (Table 2 and Figs. 1, 2) show fairly clear separation of the five families studied, as recognized by Snow (1967) and the other volumes of *Check-list of the Birds of the World*. Figure 1, however shows some overlap between Polioptilidae and Aegithalidae on these 18 characters, as does Fig. 2 on Paridae and Remizidae. In Fig. 2 the family-enclosing line of Remizidae is drawn on the simplest assumption; it could have been drawn in a bipolar shape to exclude the overlap area with Paridae.

Summarizing the 22 characters analyzed separately above, the skeleton of *Auriparus* agrees with that of *Anthoscopus* in 20 characters, *Remiz* in 19, *Parus* and *Melanochlora* in 12, *Coereba* in nine, *Psaltriparus* in eight, *Polioptila* in seven, *Aegithalos* in six, *Rhamphocaenus* and *Microbates* in five. (Partial or irregular agreement is counted the same as disagreement here.) Similarity to wrens and creepers is slight on the basis of incomplete data. I conclude that skeletal characters agree with the behavioral, nest, and external structural characters mentioned by Cramp & Perrins (1992) and tend to confirm the classification of Snow (1967). The Verdin belongs with the penduline tits, Remizidae.

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